

A FURTHER NEW GENUS OF PRIMITIVE PHORID FLY (DIPTERA: PHORIDAE) FROM BALTIC AMBER AND ITS PHYLOGENETIC IMPLICATIONS

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ABSTRACT. A new genus and species of primitive phorid fly preserved in Baltic amber, *Ulrichophora lobata*, is described. It is compared to the similar *Archiphora robusta* (Meunier) from Baltic amber and the extant *Archiphora patagonica* Schmitz, from which it differs most notably by the well-developed anal lobe and the setation of the scutum. This latter character and its possible phylogenetic utility are discussed in relation to other extinct and extant phorids. Further observations on the holotype of *A. robusta* indicate that it is probably not congeneric with the extant *A. patagonica* (Schmitz), and *A. robusta* is given the new generic name *Hennigophora* (new combination). A key to the Baltic amber sciadocerines is given. A definition is given of a new, currently rankless group, Euphorida, which includes all Phoridae except Sciadocerinae and Prioriphorinae.

INTRODUCTION

The primitive phorids classified in the subfamilies Sciadocerinae (formerly family Sciadoceridae; Disney, 2001) and Prioriphorinae are a fascinating assemblage of mostly extinct forms with a previously unsuspected diversity. New discoveries of these primitive phorids have been made recently (Mostovski, 1996, 1999; Arillo and Mostovski, 1999; Grimaldi and Cumming, 1999; Brown, 2002; Grimaldi et al., 2002) from various Mesozoic and Cenozoic amber deposits, and more are likely to be found (e.g., figures in Grimaldi and Engel, 2005). In their structure, these flies bridge some of the gaps between the two extant species of sciadocerines—*Sciadocera rufomaculata* White, 1916, from Australia and New Zealand, and *Archiphora patagonica* Schmitz, 1929, from Chile—and the other extant species of the large family Phoridae. Their large and increasingly better-known structural diversity both provides information on the evolution of these groups and confounds our understanding of their history.

With the acquisition for study of three newly collected specimens of sciadocerines from late Eocene Baltic amber (Larsson, 1978), I began to review the structure of the oldest-known Baltic sciadocerine, *Archiphora robusta* (Meunier, 1905). After close examination, I realized that there were some inaccuracies in Hennig's (1964) redescription of this species, that some of the supposed similarities with *A. patagonica* were

incorrect, and that the three new specimens represented a new taxon. The ramifications of these observations are explored in this paper.

METHODS AND MATERIALS

Amber specimens were examined and photographed while immersed in heavy mineral oil. Scanning electron micrographs (SEMs) of extant specimens were made with a Hitachi S-3000N SEM and standard coating procedures. Images of all specimens were deposited in Morphbank (www.morphbank.net). Structural terms used are those of J. McAlpine (1981).

SYSTEMATICS

Family Phoridae Curtis, 1833

Subfamily Sciadocerinae Schmitz, 1929

Ulrichophora new genus

DIAGNOSIS. Sciadocerinae. Scutum with many setulae and few dorsocentral setae only; lacking acrostichal setae (Fig. 1). Wing with well-developed anal lobe (Figs. 4, 5).

The other sciadocerine genera—*Archiphora* Schmitz, 1929, *Eosciadocera* Hong, 1981, and *Sciadocera* White, 1916—differ in having scuta with well-developed, complete rows of dorsocentral and acrostichal setae, and in lacking random setulae on the scutum.

TYPE SPECIES. *Ulrichophora lobata* new species.

Ulrichophora lobata new species

Figures 1–5

DESCRIPTION. Body length 2.6–2.7 mm. Frons approximately one-third head width (Fig. 1); lacking medial furrow; with one pair inner vertical, one pair ocellar, one pair reclinate

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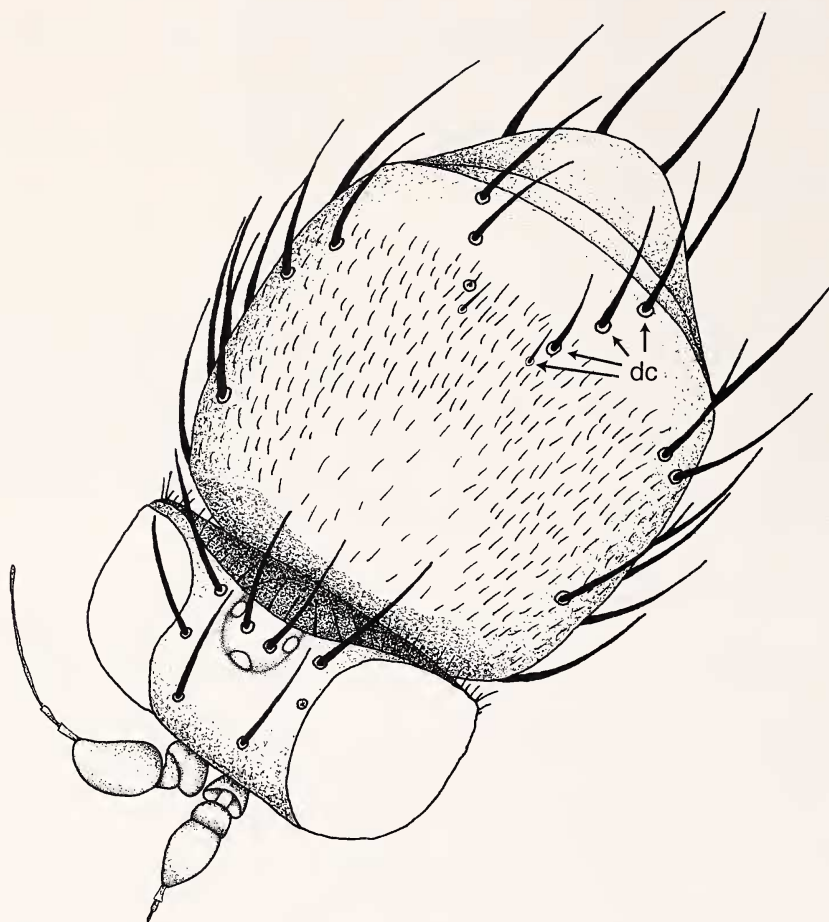


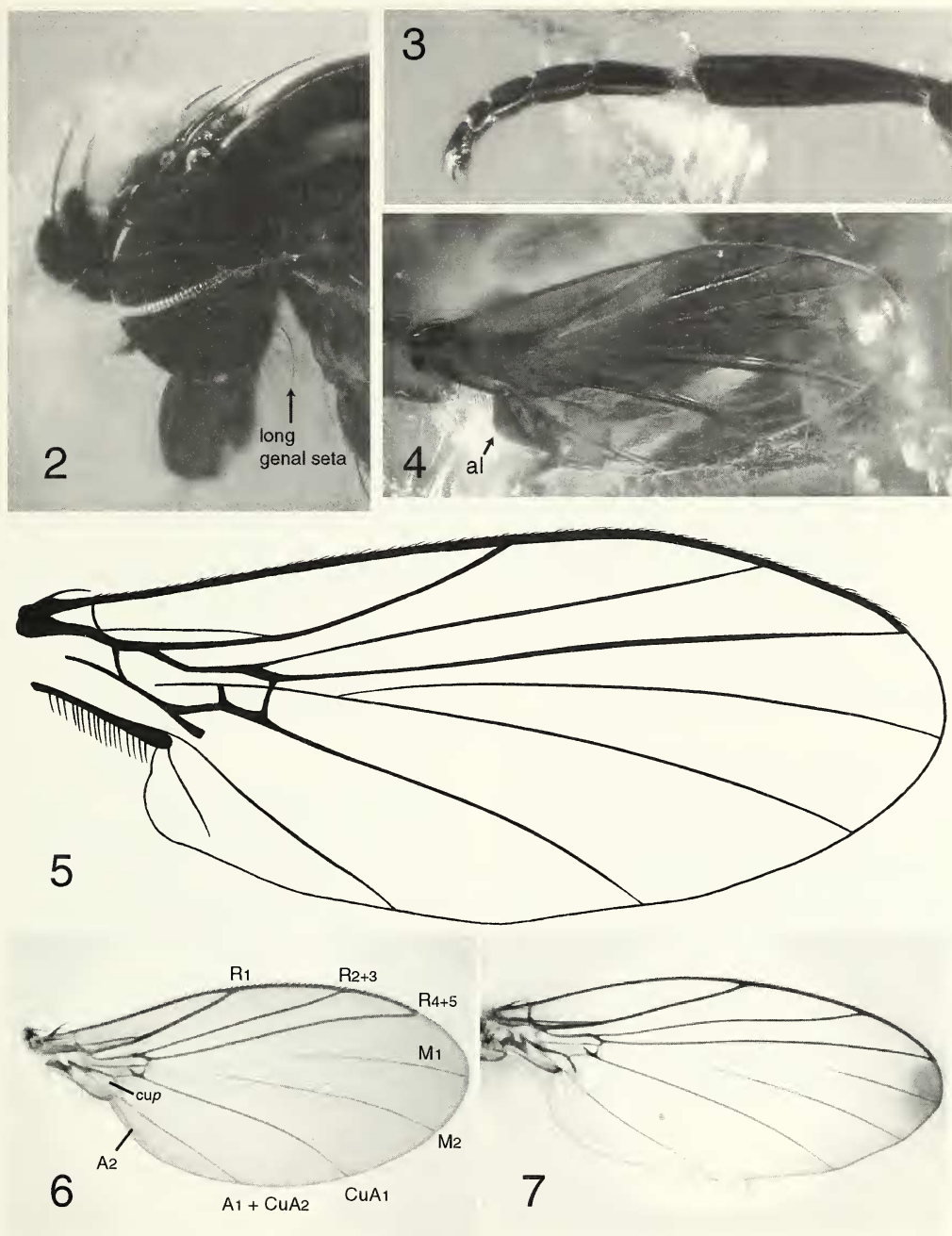
Figure 1 *Ulrichophora lobata* new species, holotype male, head and thorax, dorsal. ABBREVIATION: dc – dorsocentral setae

fronto-orbital setae near dorsal one-third, one pair interfrontal setae near midlength. Complete row of postocular setae present. One extremely long, curved genal seta present on posteroventral margin of head (Fig. 2). Flagellomere 1 of antenna elongate-oval (Figs. 1, 2), slightly pointed at apex, not greatly enlarged; arista slightly dorsal of apex. Palpus extremely small. Labellae of proboscis enlarged, expanded, bare (Fig. 2). Scutal disk dorsocentrally with small, even setulae; four posterior dorsocentral setae present, anteriormost of which is only slightly larger than scutal setulae, second seta slightly larger, setae 3–4 much larger (Fig. 1), row converging anteriorly; two intra-alar setae: one in anterior one-third (which might belong to another row, being relatively ventral in position), the second in posterior one-third; two posterior supra-alar setae present; one large basal postpronotal seta present; notopleuron with four long setae. Scutellum with two pairs of large setae. Anepisternum without setae. Foretibia with one short antero-dorsal seta near apex; tarsomeres as in Figure 3. Mid- and hind leg with anteroventral seta on

apical one-third of femur; tibia with anterior seta near midlength. Tibiae without dorsal longitudinal setal palisades (found in many Phoridae); longitudinal setal palisades present on at least fore- and hind tarsomere 1 (visible in holotype). Empodium not visible, possibly absent. Wing as in Figures 4 and 5; similar to that of extant sciadocerines (Figs. 6, 7) except more elongate; costa extends nearly to wing tip; base of M_{1+2} present; CuA_2 present; numerous (about 20) alular setae present; anal lobe large; entire surface of wing microtrichose. Venter of abdomen with well-developed setose sternites. Male terminalia small, details difficult to observe, best seen on left side of holotype.

HOLOTYPE. ♂, RUSSIA: Kaliningrad, Baltic amber (catalog number LACM ENT 159890) (Natural History Museum of Los Angeles County).

PARATYPES. ♂, GERMANY: Bitterfeld amber (private collection Paulson); one specimen (sex indeterminate; specimen is largely obscured), Baltic amber (Zoologisches Forschungsmuseum A. König, Bonn).



Figures 2–7 Sciadocerinae. 2–4. *Ulrichophora lobata* new species (Paulson specimen). 2. Head, left lateral. 3. Foretarsomeres, lateral. 4. Right wing (photograph). 5. Right wing (drawing). 6. *Archiphora patagonica* Schmitz, male, wing. 7. *Sciadocera rufomaculata* White, male, wing. ABBREVIATION: al – anal lobe

ETYMOLOGY. This name is in honor of Dr. Hans Ulrich (Bonn), who kindly lent me his specimen of *U. lobata*, and who has been highly supportive of my phorid studies.

CLASSIFICATION. Relationships among the primitive Phoridae are not well resolved. The subfamily Sciadocerinae is only weakly supported in most analyses (Brown, 1992; Grimaldi and Cumming, 1999; Mostovski, 1999) and outside of

the two extant species might not be monophyletic. A full revision of these groups is outside the scope of this paper, but for now *U. lobata* can be classified in a questionably monophyletic Sciadocerinae.

IMPLICATIONS OF THE NEW GENUS

The description of the new genus of sciadocerine phorid has implications for four subjects dis-

cussed herein: the value of scutal setation in phylogenetic reconstruction of the lower Cyclorhapha; status of the genus *Archiphora*; monophyly of the Sciadocerinae and Prioriphorinae; and monophyly of a group within the Phoridae, exclusive of Sciadocerinae and Prioriphorinae.

SETATION OF THE SCUTUM

The setation of the scutum of the new species is of interest in relation to that of other phorids and related families. Specifically, the presence of acrostichal and dorsocentral setal rows, and of scattered, random setulae, varies widely. The evolution of these setation patterns was treated in a paper by Simpson et al. (1999), but this treatment omitted detailed analysis of the lower cyclorhaphan families (=“Aschiza”), including phorids.

The composition of the non-monophyletic lower Cyclorhapha (whose status was reviewed by Yeates and Wiegmann, 1999) is controversial. Syrphidae and Pipunculidae appear to be more closely related to the Schizophora than to other lower Cyclorhapha, have random long scutal setae, and are not treated in further detail here. Opetiidae are questionably related to the Platypezoidea (Collins and Wiegmann, 2002) and might be basal to the entire Cyclorhapha; furthermore, composition of the Platypezoidea is contentious (Cumming et al., 1995; Collins and Wiegmann, 2002).

Hennig (1979) noted the tendency of Platypezidae, Sciadoceridae and Phoridae to develop a single median row of acrostichal setae, but cautioned that the direction of change from random setulae to single row of acrostichal setae (or vice versa) was not established, and might have occurred more than once.

States of scutal setation for the various families are reviewed below, with special emphasis on the acrostichal and dorsocentral rows and on the presence of random setulae.

Asiloidea (outgroup taxon) – The Asiloidea, or a portion therein, is considered to be the sister group to the Eremoneura (Sinclair et al., 1994). There is a single median row of acrostichal setae in some genera in this group (for example, in at least some species of the dasypogonine asilid genera *Blepharepium* Rondani, 1848, and *Callinicus* Loew, 1872), some have differentiated dorsocentral setae, and some have scattered dorsal random setulae, with or without differentiated dorsocentral setae.

Empidoidea (outgroup taxon) – In the various groups of Empididae and Dolichopodidae there are different types of scutal setation present: random setulae without large dorsocentral and acrostichal setae (as in some fossils illustrated by Grimaldi and Cumming, 1999), one acrostichal row, and two acrostichal rows (Sinclair and Cumming, 2006).

Schizophora (outgroup taxon) – Various states are found in this group, although a thorough review is beyond the scope of this paper. Some have random setulae and large marginal setae (as in extant phorids); some have a single median row of acrostichal setae, as in some acalyptrates: *Leiomyza* Macquart, 1835 (Asteiidae), *Stenomicro* Coquillett, 1900 (Periscelididae), some *Aulacigaster* Macquart, 1835 (Aulacigastridae), *Nemo* D. McAlpine, 1983 (Neminiidae), *Neomeoneurites* Hennig, 1972 (Carnidae); many have two acrostichal rows (for example in most calyptrates).

Chimeromyia Grimaldi and Cumming, 1999 – The three species of these strange flies were placed in the Eremoneura (Empidoidea + Cyclorhapha), although with family unknown, by Grimaldi and Cumming (1999). There is a single median row of acrostichal setae, plus the usual lateral rows of dorsocentral setae; random setulae are apparently absent.

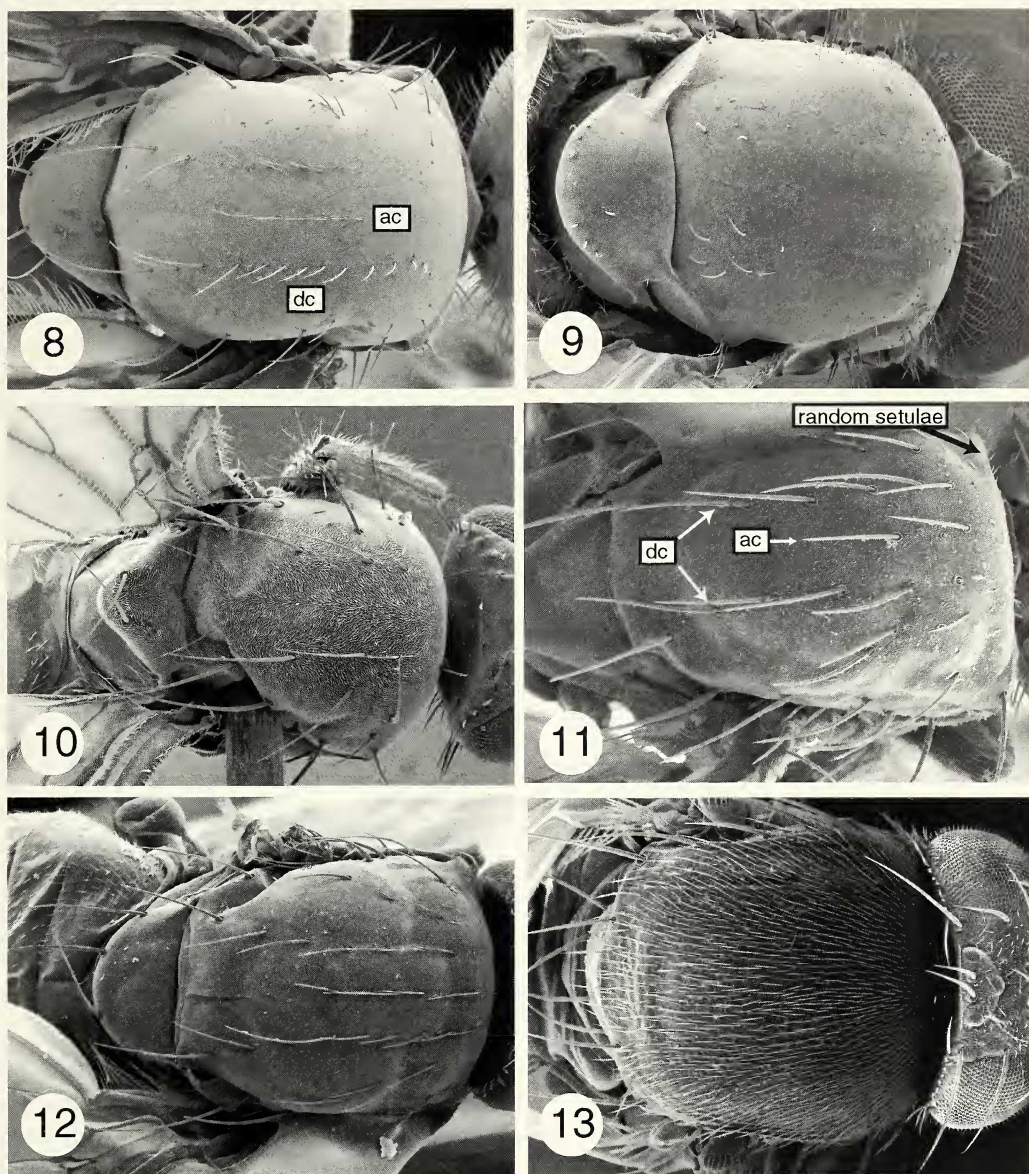
Opetiidae – According to Chandler (2001: fig. 3) *Opetia nigra* Meigen, 1830, has random small setulae, no acrostichal setae, and larger dorsocentral setae similar to those of *U. lobata*, except that the dorsocentral row is more complete anteriorly. There are about six differentiated dorsocentral setae, of which the posterior two are clearly larger.

Platypezidae – The setae of the dorsum of many extant platypezids are organized into rows, sometimes with a single medial acrostichal row, a dorsocentral row, and fewer intra-alar and supra-alar setae (Fig. 8). The medial setae (acrostichal and most dorsocentral), however, are clearly smaller than the larger peripheral setae, and the acrostichal row is often absent (Fig. 9). Random setulae are absent.

An exception to the general conditions found in platypezids is one possible fossil platypezid, *Electrosania cretica* (described by Grimaldi and Cumming, 1999), in which there are random setulae, and in which dorsocentral and acrostichal rows are lacking. The placement of this species in Platypezidae is controversial, however, as it has some unusually primitive characters.

Lonchopteridae – Extant species of this family, all of which are in the genus *Lonchoptera* Meigen, 1803, lack random setulae, lack acrostichal setae, and have relatively few, large dorsocentral setae (Fig. 10). Cretaceous fossil genera described by Grimaldi and Cumming (1999) apparently also have dorsocentral setae, but the full setation of the scutum cannot be seen.

Ironomyiidae – There are three extant species of *Ironomyia*: *I. nigromaculata* White, 1916 and two undescribed species (D. McAlpine, in press). In a recent review of the group, D. McAlpine (in press) noted that these species displayed many to no long, pilose dorsal setulae, and large marginal setae only. In the Cretaceous fossil *Cretonomyia pristina* J. McAlpine, 1973, there are small



Figures 8–13 Scutum, SEMs. 8. *Grossoseta pacifica* (Kessel) (Platypzeidae). 9. *Polyporivora polypori* (Willard) (Platypzeidae). 10. *Lonchoptera* sp. (Lonchopteridae). 11. *Archiphora patagonica* Schmitz (Sciadocerinae). 12. *Sciadocera rufomaculata* White (Sciadocerinae). 13. *Megaselia* sp. (Phoridae). ABBREVIATIONS: ac – acrostichal setal row, dc – dorsocentral setal row

random setulae, and few small marginal setae (J. McAlpine, 1973). Other fossils occur (Mostovski, 1995; Grimaldi and Cumming, 1999), but D. McAlpine (in press) had doubts that they were related to *Ironomyia* and *Cretonomyia*; furthermore, he questioned whether this family was related to the others considered here. Molecular analysis should help answer this question, and it is unfortunate that the study of Collins and Wiegmann (2002) did not include a specimen of this family.

Cretaceous phorid fossils – There are many taxa described in the non-monophyletic morass of

fossils classified in the Sciadoceridae (now Sciadocerinae) and Prioriphorinae; the latter is a holding place erected by Mostovski (1996) for those taxa that more closely resemble phorids. Fossil phorids have not always been documented in sufficient detail for this character.

Agaphora rara Mostovski, 1999 – According to Mostovski (1999), there is a single median acrostichal row and dorsocentral rows, but the setae are relatively small except for that on the posteriormost dorsocentral aspect, which is twice the length of the others. No mention is made of random setulae. The scutal setation of the other

species in this genus, *A. iunior* Mostovski, is not mentioned.

Archiphora pria Grimaldi and Cumming, 1999 – The scutum of this species is obscured and cannot be reliably characterized.

Archisciada lebanensis Grimaldi and Cumming, 1999 – There are random setulae on the scutum of this species.

Euliphora grimaldii Arillo and Mostovski, 1999 – In their drawing (Arillo and Mostovski, 1999:fig. 2) and description of this species, the scutal setation is interpreted as setae in irregular rows, including a pair of acrostichal rows. The photograph of this species (Arillo and Mostovski, 1999:fig. 1), however, shows what I consider random setulae on the scutum, with larger marginal setae.

Gemmaphora numerosa Mostovski, 1999 – According to Mostovski (1999), there is a median row of minute acrostichal setae (irregular anteriorly), 12 dorsocentral setae, and random setulae. Presumably, the random setulae are anterolateral, as in *Archiphora patagonica* (Fig. 11).

Maksika duija Mostovski, 1999 – According to Mostovski (1999), there is a single median row of acrostichal setae and a well-developed dorsocentral row. No mention is made of random setulae.

Prioriphora canadambra McAlpine and Martin, 1966 – The original description of this species depicts the scutum as having a platypezid-like setation, with a single median acrostichal row, and complete dorsocentral rows. Smaller setae are depicted on the anterolateral corners only.

Prioriphora casei Grimaldi and Cumming, 1999 – This species has random setulae on the scutum, similar to those of most extant phorids.

Prioriphora cheburashka Mostovski, 1999 – According to Mostovski (1999), this species has nine to 10 acrostichals in a single median row, nine to 10 dorsocentral setae, and random setulae on the scutum.

Prioriphora intermedia Brown and Pike, 1990 – This species has a single median acrostichal row, and well-developed dorsocentral rows. No mention is made of random setulae (Brown and Pike, 1990).

Prioriphora luzzi Grimaldi and Cumming, 1999 – According to the description of this species, there is a single median acrostichal row, as well as a pair of paramedial acrostichal rows anteriorly, and scattered acrostichals. I have not seen a specimen of this species, and the thorax is not figured, so the extent of the dorsocentral setae (which are briefly mentioned) is unknown.

Prioriphora polyanka Mostovski, 1996 – This species has a single median acrostichal row of nine setae, plus a row of nine dorsocentral setae (with the posterior dorsocentral setae larger). Mostovski's original description (Mostovski, 1996) indicated that there were two acrostichal rows, but he later corrected this error (Mostovski, 1999). There are no random setulae indicated.

Prioriphora spp. – The descriptions of *P. longicostalis* and *P. setifemoralis* by Brown and Pike (1990) noted that the scutal setation cannot be seen in these specimens.

Sciadophora bostoni McAlpine and Martin, 1966 – This species has long scutal setae, organized in a single medial acrostichal row and two complete dorsocentral rows. No random setulae are present.

This fossil was incorrectly listed as being deposited in the Canadian National Collection in the original description (McAlpine and Martin, 1966). In fact, it was retained by the collector, who subsequently sold it to the author. It is now deposited in the Los Angeles County Museum (LACM). In order to stabilize the fossil, it has been mounted in a block of clear epoxy.

Varya lalita Mostovski, 1999 – The original description (Mostovski, 1999) mentions well-developed dorsocentral setae, but no others.

Myanmar amber phorid – The LACM collection has one, as yet undetermined, specimen of phorid from Myanmar amber. It has wing venation similar to that of specimens illustrated by Grimaldi et al. (2002) as *Prioriphora* sp. This specimen has large marginal setae, plus random setulae, as in modern phorids.

Tertiary phorid fossils – *Eosciadocera helodis* Hong, 1981 and *E. setosa* Brown, 2002 – These two species have a single median acrostichal row, well-developed dorsocentral and intra-alar rows, and are without random setulae.

Ryszard Szadziewski has an additional specimen of *E. setosa* in which he can see a well-developed empodium (R. Szadziewski, personal communication). The lack of an empodium is a character used by McAlpine (1989) to justify the family Sciadoceridae, but he noted that it is also absent in Lonchopteridae. Grimaldi and Cumming (1999) used this character to define the Sciadoceridae, exclusive of their fossil *Archisciada lebanensis*. Based on their analysis, *Eosciadocera* should also be excluded and placed near the base of their Sciadoceridae.

Archiphora robusta (Meunier) – I re-examined the holotype of this species (see further discussion, below). The scutum has three acrostichal setae in a single median row, and six dorsocentral setae. There are a few (fewer than 10) smaller setae in the anterolateral corner, similar to those in *A. patagonica*, *P. canadambra*, and *S. rufomaculata*.

Extant Sciadocerinae – These flies have well-developed dorsal rows of setae, almost entirely without setulae. In *Sciadocera* there is a single median acrostichal row, two dorsocentral rows, and two intra-alar setae (Fig. 12). In *Archiphora* the acrostichal row is represented by two (Fig. 11) to four setae only; otherwise it is similar to *Sciadocera*.

Extant phorids (except sciadocerines) – Most have small even setulae on the dorsum of the scutum, with larger setae mostly marginal in

position (Fig. 13). Each setula is clearly socketed (Fig. 14). Some phorids have a few extra dorso-central setae (e.g., Fig. 15), up to four in total (Schmitz, 1938). Disney (2001) noted some phorids lack the small setulae of the thorax, but this is likely a secondary loss at least in some social insect-associated species (*Platydipteron* Borgmeier and Prado, 1975, *Laishania* Kung and Brown, 2005). In *Platydipteron balli* Brown, 1994 (Fig. 16), for example, there are scattered large setae without the small setulae. Schmitz (1938) wrote that the scutal setae sometimes become bristlelike between the posterior dorso-central setae, and more rarely along the median line, which he referred to as a single row of acrostichal setae. Unfortunately, he did not name any taxa with this character, so I could not examine it, but it must be extremely rare. Some species of the genus *Hypocera* Lioy, 1864, have a pair of marginal (posterior) setae medial to the usual dorsocentral setae that I (Brown and Buck, 1998; Brown, 1999) named acrostichal setae. These are present only as a pair of posterior setae on the scutum, however, and do not form rows; probably they are an autapomorphic development within these species.

In the phorid subfamily Termitoxeniinae some minute species are without setulae on the scutum and instead have scattered (or poorly organized) larger setae and no setulae (Fig. 17); however, some larger termitoxeniine species have the usual random setulae and larger marginal setae. There are some molecular data linking termitoxeniines with the genera *Dohrniphora* Dahl, *Diploneura* Lioy, and *Thaumatoxena* Breddin and Börner (Cook et al., 2004), but in our preliminary molecular data (Brown and Smith, in preparation) using many more genes and taxa, the same species come out in a much different part of the tree. For now I simply note the possibly primitive state found in this group.

SUMMARY OF SCUTAL SETAE IN CYCLORRHAPHA

Based on this review of the scutal setae of lower Cyclorrhapha, it is possible to generalize (as did Hennig, 1979, and Sinclair and Cumming, 2006) that a single acrostichal row, or the tendency to develop such a row, is primitively present in Platypezoidea (based on its presence in Sciadocerinae, some Prioriphorinae, and some Platypezidae) although it is absent in some taxa (Opetiidae, Lonchopteridae, Ironomyiidae, most Phoridae).

The presence of a single row of acrostichal setae is in contrast to the paired acrostichal setae found in many Schizophora, although a single row is found in some schizophoran taxa. Thus, the conclusion of Simpson et al. (1999:p. 1354) that the pattern for Cyclorrhapha was set in the common ancestor of the group is not entirely correct, as there was apparently one group

tending towards a single acrostichal row (Platypezoidea) and another towards two rows (Schizophora).

Based on developmental evidence, it is probable that the presence of two acrostichal setal rows is a more primitive character state than having just one row (P. Simpson, Cambridge University, personal communication). The thorax is derived from two physically separated imaginal discs, and the two halves of the adult notum fuse along the dorsal midline just before pupation when precursors for the bristles are already formed. Thus, there cannot be a single median row at the time of formation of bristle precursors. Simpson (personal communication) assumes, but has not directly visualized, that a single row must arise from movement of the precursors from a row on either side that align to form a single one. Analogous limited movement of precursors of microchaetes (=setulae of this paper, and which form rows in some Drosophilidae) has been shown to take place in *Drosophila* (Renaud and Simpson, in press).

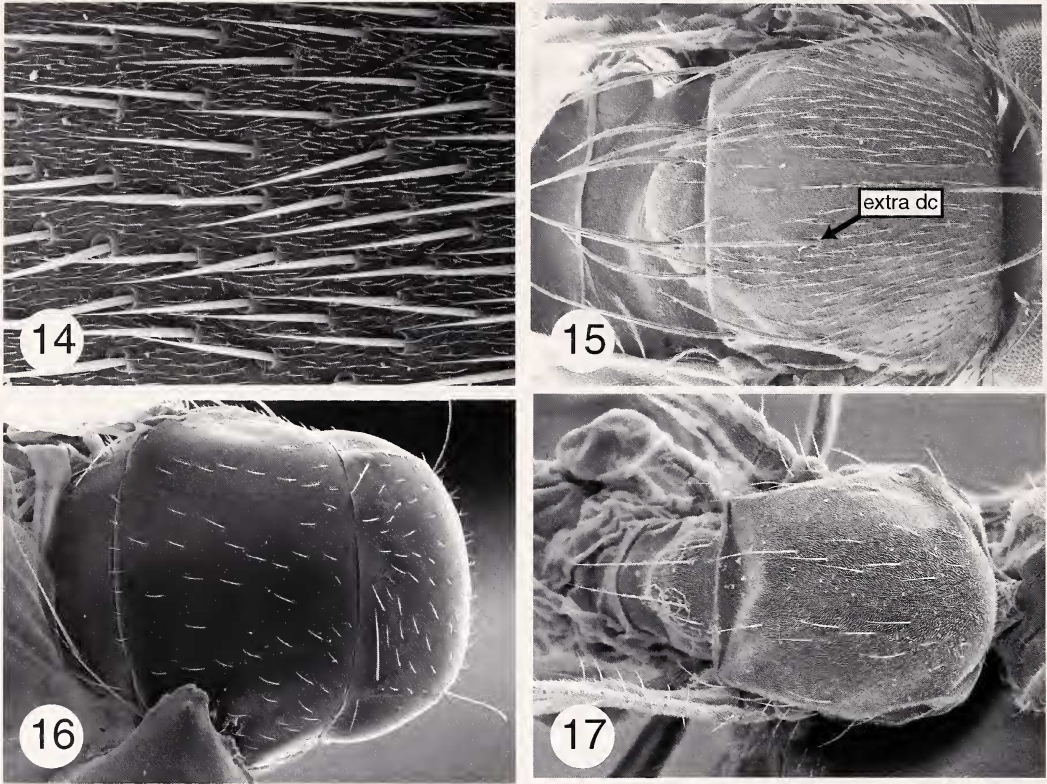
Hennig (1979) stated that the direction of evolution of scutal setation in the Phoridae seemed to indicate that random setulae and no acrostichal row seems to have evolved from ancestors lacking random setulae and with a single median acrostichal row. The descriptions of *Euliphora*, *Gemmaphora*, *Ulrichophora*, and the Burmese phorid, however, shows that the situation is even more complicated, with some sciadocerine-like flies having the same characters as the more derived extant phorids.

Of the families of Platypezoidea, nearly all have some taxa with random setulae and some taxa with a single median row of acrostichal setae; the exceptions are Lonchopteridae, which lack random setulae and acrostichal setae (contrary to Simpson et al. [1999] who stated all "Aschiza" have species with random setulae), and Ironomyiidae, which lack dorsocentral and acrostichal setae; possibly Platypezidae should be added to this list, depending on the classification of *Electrosania*. Where the presence or absence of random setulae or acrostichal setae is derived or primitive is not yet known, but the presence of random setulae and acrostichal setal rows seems to be mutually exclusive. Further research is needed, incorporating these and other characters into phylogenetic analyses.

IMPLICATIONS FOR GENUS ARCHIPHORA SCHMITZ

Hennig (1964) placed Meunier's *Napomyza robusta* in the genus *Archiphora* based on two characters: the reduced anal lobe (which he referred to as axillary lobe or "axillarappen"), and the reduced cell cup (=anal cell).

The anal lobe is indeed reduced in both *Archiphora patagonica* and *A. robusta*. By itself,



Figures 14–17 Phoridae, scutum, scanning electron micrographs. 14. *Megaselina* sp. (higher magnification). 15. *Spiniphora maculata* (Meigen). 16. *Platydipteron balli* Brown. 17. *Termitophilomyia zimbraunsi* Disney

however, it is a relatively weak synapomorphy of the genus; such reduction occurs in many taxa and is widespread in Phoridae. The wing of the two species is similar in shape (short, rounded), another possible character linking them, although one that might be functionally linked to the reduced anal lobe.

The reduction of cell cup is not a valid synapomorphy of *Archiphora*. A comparison of a wing photograph of a male *A. patagonica* (Fig. 6) with that of a male *Sciadocera rufomaculata* (Fig. 7) shows that this cell is equivalent in the two extant species. In my re-examination of the specimen of *A. robusta* I was able to obtain a different view from Hennig's (1964:fig. 5) drawing, and found that cell cup is much larger (see Fig. 18) than portrayed in Hennig's figure. This character is thus shown to be completely spurious.

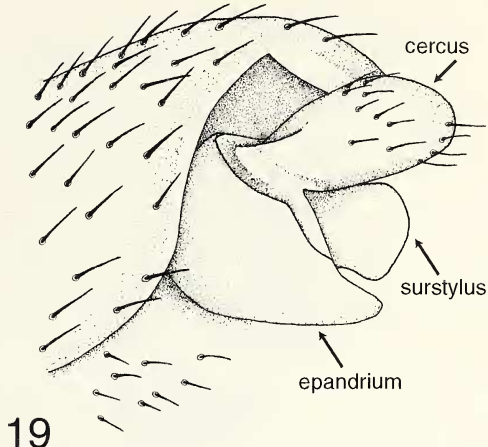
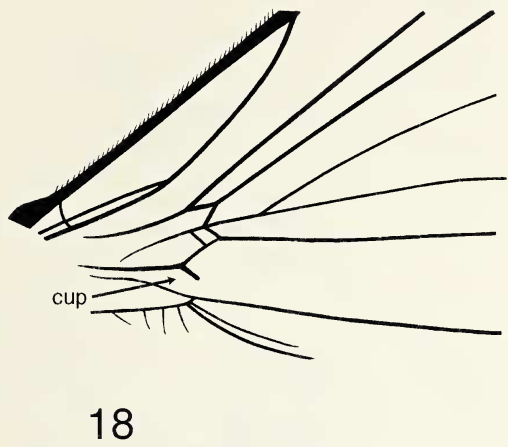
Hennig (1964) declared the specimen of *Archiphora robusta* to be a female. In my opinion this is incorrect; the terminalia are indeed small, but they are also small in males of *A. patagonica* and *Sciadocera rufomaculata*. Furthermore, in ventral view details are visible that show the specimen is a male, particularly the presence of large, median cercal lobes and epandrium- and surstylus-like sclerites (Fig. 19).

The determination that the specimen of *A. robusta* is a male greatly undermines the case for

Archiphora patagonica and *A. robusta* being congeneric. A synapomorphic character state of the two extant sciadocerines, *A. patagonica* and *S. rufomaculata*, is that flagellomere 1 of males is greatly enlarged (although this character also occurs widely in the Phoridae), with a coincident reduction in the length of the frons and the loss of the interfrontal seta. In the single specimen of *A. robusta*, flagellomere 1 is small, the frons is long, and the interfrontal seta is present (Hennig, 1964:fig. 10).

In both extant species, *A. patagonica* and *S. rufomaculata*, the common base of wing veins M_1 and M_2 is reduced (Figs. 6, 7); in *S. rufomaculata* it is virtually absent. This is another potential synapomorphic character of the two species. In contrast, the medial base in *A. robusta* is apparently well developed. Therefore, recognition of *A. robusta* as part of genus *Archiphora* would render the genus paraphyletic (Fig. 24).

With limited evidence to link *A. patagonica* and *A. robusta*, and noting the possible synapomorphic characters of *A. patagonica* and *S. rufomaculata*, I propose a new genus name *Hennigophora* to include the type species *H. robusta* (Meunier) (new combination). Diagnosis of this taxon is as follows: male with flagellomere 1 relatively small; frons large, with frontal setae as in *Archiphora patagonica* (Fig. 21); scutum with



Figures 18–19 *Hennigophora robusta* (Meunier). 18. Base of wing. 19. Male terminalia, left lateral

well-developed rows of setae consisting of one median acrostichal row and one dorsocentral row on each side; base of $M_1 + M_2$ well developed; anal lobe small; empodium absent; male terminalia with separate surstylus on left side.

In order to clarify the recognition of the Baltic sciadocerines, I present the following key to species:

**KEY TO BALTIC AMBER
FOSSIL SCIADOCERINAE**

- 1. Scutum with small random setulae and only a few large dorsocentral setae (Fig. 1) *Ulrichophora lobata* n. sp.
- Scutum lacking random setulae, but with rows of large dorsocentral and acrostichal setae (as in Figs. 11, 12) 2
- 2. Frons narrow, about one-quarter head width; scutellum with 10–12 setae *Eosciadocera setosa* Brown
- Frons broader, about one-half head width; scutellum with 4 setae *Hennigophora robusta* (Meunier)

A further species of *Archiphora*, *A. pria*, was described from Cretaceous New Jersey amber (Grimaldi and Cumming, 1999). This species has a well-developed base of vein M, unlike *A. patagonica* and *Sciadocera rufomaculata*; has numerous frontal setae; has a scutum possibly with random setulae and apparently has no medial macrosetae (although the scutum is obscured). It probably should be placed in another genus.

**MONOPHYLY OF SCIADOCERINAE
AND PRIORIPHORINAE**

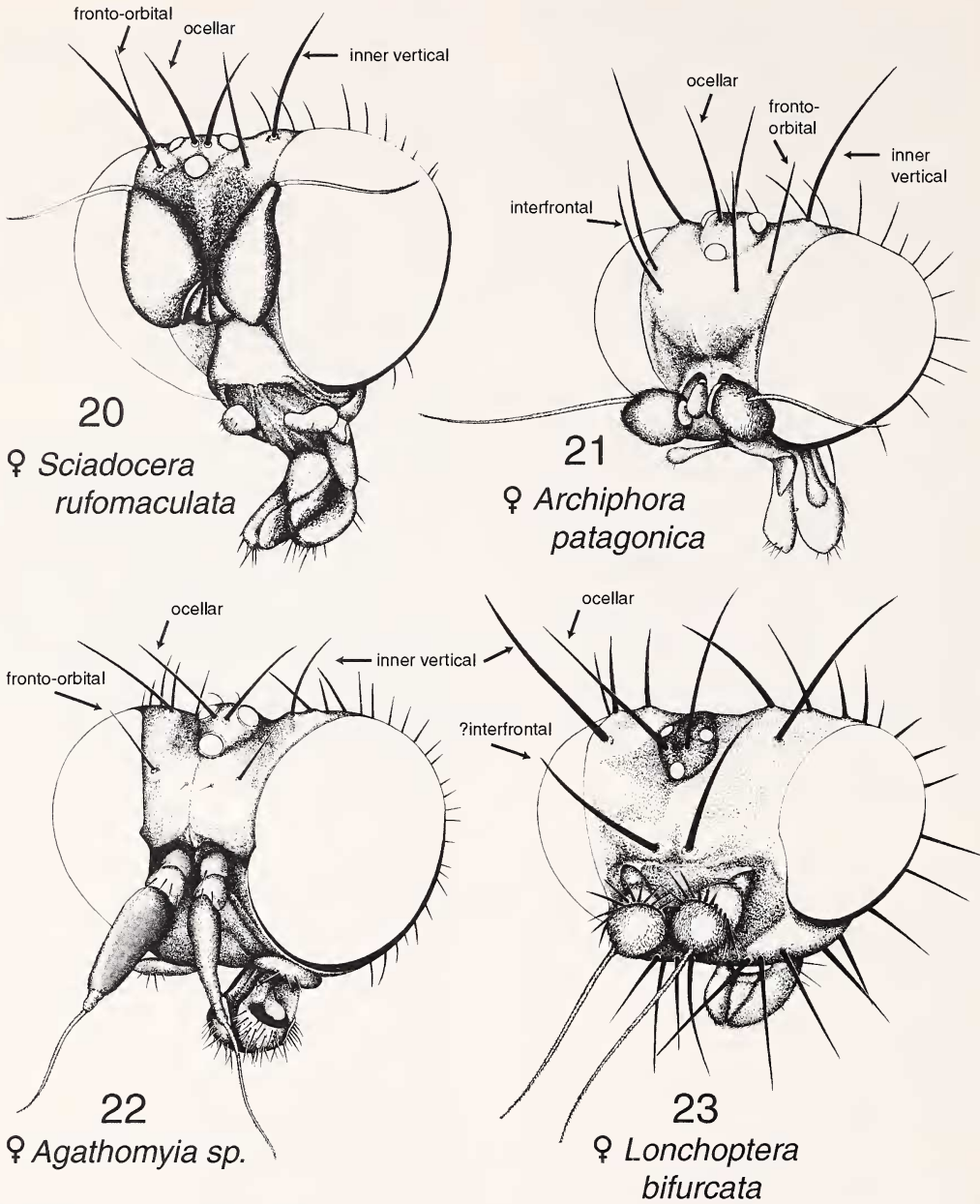
Sciadocerinae – I supported the monophyly of this group (Brown, 1992) in my revision of phorid classification with some hesitation. Of the four characters I proposed, two were internal char-

acters that are not visible in fossils. One of the other two characters, the enlarged male flagellomeres, apparently applies only to the extant species of the subfamily, as discussed above. The only remaining character is the asymmetrical male terminalia, a condition that is also widespread in many Phoridae and that is difficult to observe in amber fossils. This last character was also the one used to define Sciadoceridae by Grimaldi and Cumming (1999) in their phylogeny.

Disney (1991) proposed that the presence of enlarged anterior femoral setae on the mid- and hind legs as a synapomorphy of Sciadocerinae (as Sciadoceridae), and they are indeed present in *Sciadocera*, *Archiphora*, *Eosciadocera*, *Hennigophora*, and *Ulrichophora*. They also occur in *Lonchoptera*, however, and in some Prioriphorinae: on the midfemur of most *Prioriphora* (except *P. intermedia* Brown and Pike, 1990) and also the hind femur of *P. setifemoralis* Brown and Pike, 1990. The midfemoral seta is present in *Archisciada*, but the seta is absent from the hind femur. Unfortunately, the terminalia of *Prioriphora* fossils are not easily visible, and it is impossible to tell whether they are asymmetrical or not. It is possible that the presence of an anterior seta on the midfemur could be used to group *Prioriphora* with Sciadocerinae, but this would contradict some other hypothesized apomorphies. Further research is required, and it would be especially important to examine further specimens.

Basing the monophyly of the subfamily Sciadocerinae on the asymmetrical terminalia, an often convergent and difficult-to-observe character, is tenuous and unsatisfactory. It is possible that this “subfamily” is part of a paraphyletic stem group, in which the fork of the radial veins is still extremely long and the base of $M_1 + M_2$ is still present (although reduced in *Archiphora patagonica* and absent in *Sciadocera rufomaculata*).

Alternate views are those of Mostovski (1999) and Disney (e.g., 2001). Mostovski (1999)



Figures 20–23 Platypezoidea, heads

attempted to justify the Sciadocerinae by the presence of a poorly developed anal lobe, but also noted that both states were present in this group. This character is further undermined with the inclusion of *U. lobata*, with its large anal lobe, in the Sciadocerinae. Disney (1985 and elsewhere) maintains that the long, thin veins of most phorids are different from those in the sciadocerines, based on some mutants with unusual cross-veins that point to differing vein homologies. My disagreement with Disney's hypothesis was outlined previously (Brown, 1992).

Prioriphorinae – Mostovski (1999) proposed that the Prioriphorinae were monophyletic,

based on the absence of an empodium, a character that also occurs in some Sciadocerinae. One described species, *Euliphora grimaldii*, was classified as a prioriphorine by its authors (Arillo and Mostovski, 1999) in spite of its having an empodium. Given that some prioriphorines seem to be more similar to extant phorids (minus sciadocerines) than others, there is evidence that it is instead a grade group. It was considered a grade, or paraphyletic group, by McAlpine and Martin (1966), Brown (1992), and Grimaldi and Cumming (1999:fig. 65). See also the discussion of *Gemmaphora numerosa*, below.

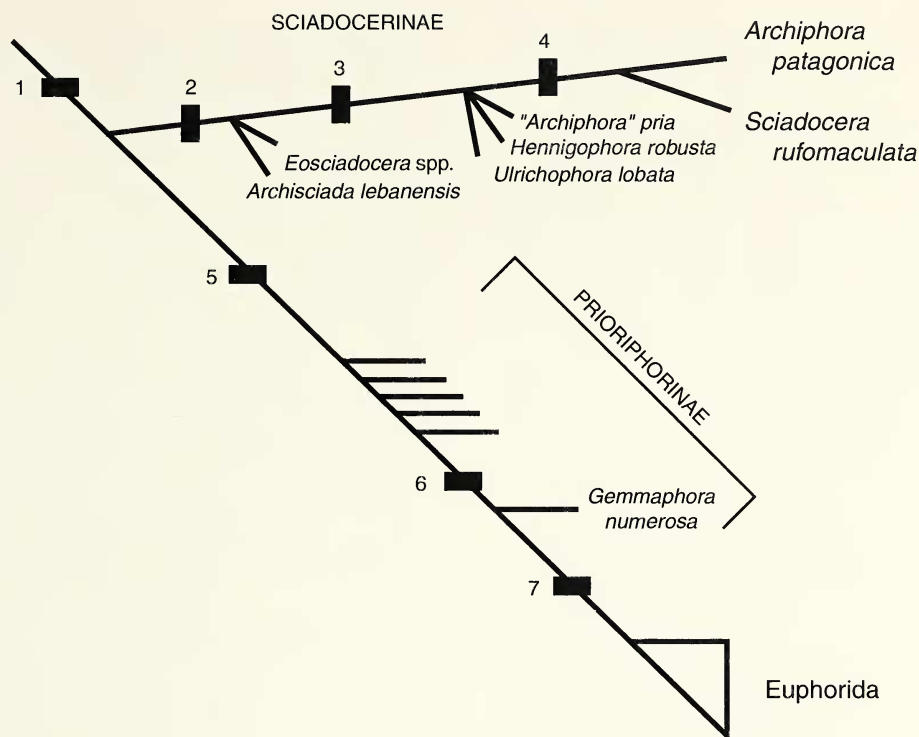


Figure 24 Cladogram of current concepts of higher relationships in Phoridae. Numbered nodes with included characters are defined in the text.

PROPOSAL AND MONOPHYLY OF GROUP EUPHORIDA

Disney (2001) questioned my 1992 definition of the Phoridae as being those taxa with a distinctive wing venation. He stated that there are subsequently described fossil taxa that span the range of this character, and his own definition using longitudinal setal palisades on hind tarsomere 1 (and thus including former Sciadoceridae) is preferable to define a family. I do not object to including the former Sciadoceridae in the Phoridae because, as I noted previously (1992), the evidence to support sciadocerid monophyly is weak. The same can be said for subfamily Prioriphorinae Mostovski, which is likely not monophyletic. However, a name and diagnosis is needed to refer to a group including the non-sciadocerine, non-prioriphorine phorids. One possibility is to call this group subfamily Phorinae and demote the current phorid subfamilies (Phorinae, Metopininae, and others) to tribes. The subfamily level has been used consistently through recent phorid history, however, for groups such as Metopininae, and until more definitive results on the internal phylogeny of Phoridae are available, I prefer to leave this ranking unchanged. Another option is to refer to this group as the Phoridae, s. str., as Sinclair and Cumming refer to their two groups Dolichopodidae s. lat. and Dolichopodidae s. str. I

prefer not to refer to two groups by the same name, however, and feel that a new term, even if it is used almost exclusively by phorid workers, is necessary. I here propose a new, currently rankless, group, the Euphorida, that includes all phorids except Sciadocerinae and Prioriphorinae. This group, which is basically equal to the extant phorid subfamilies Hypocerinae, Aenigmatiinae (including Thaumatoxeninae), Phorinae, Conicerinae, Termitoxeniinae, and Metopininae (as recognized by Brown, 1992) or extant Phoridae of Mostovski (1999), is defined as follows:

1) Dense setulae present on dorsum of scutum, and large setae mostly restricted to periphery of scutum. This character was proposed by Schmitz (1929) for the entire Phoridae at that time. There are a few apparently derived taxa that have lost the dense setulae (as discussed above), but such rare exceptions, in my opinion, do not disqualify this character as a strong diagnostic character of Euphorida. There are a few phorids that have, in addition to the posterior dorsocentral seta, one or two pairs of more anterior dorsocentral seta (e.g. some *Spiniphora* Malloch).

2) Radial veins with fork of R_{2+3} and R_{4+5} in apical third of R_s , rather than in basal one-third.

Although there are some extant phorids with long radial forks, such as *Megaselia prolixifurca* Kung and Brown, this appears to be a secondarily derived condition. Most have a short fork.

3) Frons with one pair ocellar (or postocellar), one pair of inner vertical, two pairs of interfrontal, two pairs of fronto-orbital, and one or two (occasionally more) pairs of supra-antennal setae. Some derived phorids have lost some or all of these setae, but they are present in most.

The setation of the frons is pivotal to characterizing the Euphorida. Of the outgroups, most have the condition shown in female *Archiphora patagonica* (Fig. 21; males of *A. patagonica* and *Sciadocera rufomaculata* have the frons and frontal setation reduced, in conjunction with the enlarged flagellomere 1), in which there is one pair of ocellar setae, one pair of inner vertical setae, one pair of fronto-orbital setae, and one pair of interfrontal setae; this pattern is found in *Ulrichophora* (Fig. 1) *Hennigophora*, *Euliphora*, and most *Prioriphora*. The frons of *Sciadophora* is similar to that of *Archiphora*, but there are three additional pairs of small, medial setae of unknown homology. Some taxa lack one pair of setae found in *A. patagonica*, either the interfrontal or fronto-orbital: *Agathomyia* Verrall (Platyppezidae; Fig. 22), *Lonchoptera* (Fig. 23), *Sciadocera*, and *Prioriphora polyanka*. The heads of most of Mostovski's (1999) species are not drawn, so I am not certain about their setation, but there are more setae present in a few of his taxa, such as *Agaphora* spp. and *Gemmaphora numerosa*, as well as in *Eosciadocera* spp.

The frontal setation of *G. numerosa* is especially interesting. According to the illustration of Mostovski (1999:fig. 10) there is a pair of inner and outer vertical setae, one pair of interfrontal setae, one pair of fronto-orbital setae, three small setae of unknown homology, and one pair of supra-antennal setae. This is the only known species outside of Euphorida with supra-antennal setae; however, no sciadocerine, prioriphorine, or other outgroup taxon has the stereotypical setation of the Euphorida, as described above.

4) Base of wing veins M_1 and M_2 absent.

This wing vein base is convergently absent in *Sciadocera rufomaculata*.

5) Cells cup and dm absent.

6) Venter of male abdomen with sclerites absent.

Ventral abdominal sclerites are present in *Sciadocera*, *Archiphora patagonica*, *Hennigophora*, *Ulrichophora*, and possibly *Prioriphora canadambra*. Unfortunately, it is not reported in other fossils.

7) Abdomen without thin sclerite between tergite 6 and terminalia (present in *Sciadocera* and *Archiphora*).

Unfortunately, this sclerite is not easily observed in most fossils.

8) Empodium present.

The empodium is absent in *Sciadocera*, *Archiphora*, *Hennigophora*, *Ulrichophora*, and most

prioriphorines, but it is present in *Archisciada*, *Eosciadocera*, and *Euliphora*.

9) Femora without large setae.

There are a few relatively derived Euphorida that have large femoral setae (for example *Melaloncha* Brues and *Melittophora* Brues), but nearly all lack them.

The results of the character discussions in this paper are hand-plotted on the tree in Figure 24, which is also based on Brown (1992:fig. 5C) and Grimaldi and Cumming (1999:fig. 65). The hypothesized synapomorphic characters of each node are listed below:

Node 1 (defining Phoridae) – Hind basitarsus with longitudinal setal palisades (Disney, 2001). Although this character has not been widely reported in fossils, it is present at least in *Hennigophora*, *Ulrichophora*, and *Sciadophora*. Several further characters for this node were given by Brown (1992:pp. 13–15, characters 1b, 3–7, 8a, 9–14; also see fig. 5C); of these, character 11 (great reduction or loss of base of $M_1 + M_2$) is now considered valid at nodes 4 and 5 in Figure 24 (although there has apparently been some reversal, such as in *Prioriphora luzzi*; see Grimaldi and Cumming, 1999:fig. 57). Many of these characters are not visible in fossils.

Node 2 (defining Sciadocerinae) – Male terminalia asymmetrical. This character has only been confirmed in *Archiphora*, *Sciadocera*, and *Archisciada*. It has not been reported in any prioriphorine.

Node 3 – Empodia absent. Also absent in most Prioriphorinae.

Node 4 (defining extant Sciadocerinae) – Male flagellomere 1 enlarged and frons reduced; base of wing veins $M_1 + M_2$ reduced or absent.

Node 5 (defining Prioriphorinae + Euphorida) – Radial veins thickened; anal lobe reduced; CuA_2 lost; cup lost; base of $M_1 + M_2$ shifted anteriorly.

Node 6 – Supra-antennal setae present.

Node 7 (defining Euphorida) – Fork of radial veins short; modern phorid frontal setation (as defined above). Scutum with random setulae, without acrostichal setae. Femora without large setae.

The proper placement of some characters, such as ventral sclerites in males, awaits further study of fossils. Many further nodes should be established, especially in the prioriphorines, and some characters will probably have to be moved to other nodes as more information becomes available.

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